

Capture-recapture and evolutionary ecology: further comments

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Introduction

Most of the points that were important to bring to statisticians' attention have already been nicely described by Cooch *et al.* (this issue) and Nichols (this issue). Natural selection and adaptation are certainly the central tenets of evolutionary ecology and require measuring differences in fitness components or differences in combined components of fitness components. However, the biological significance of any difference in fitness is complicated by technical as well as theoretical considerations.

Heterogeneity and evolutionary ecology

Indeed, it is now widely recognized that individual variability is a rule rather than an exception. Besides well-known sources of heterogeneity such as age, sex, size, weight, etc, individual variability is generated by differences in the genetic architecture, maternal history, the environments encountered during phenotypic development and all these levels of heterogeneity likely to interact to shape the values of the fitness components at any time during the individual's life history.

Maybe a first step towards tackling the problem of heterogeneity is to try to recognize at which levels individual heterogeneity is generated. Two axes, not necessarily mutually exclusive, might organize most individual heterogeneity: space and history. Local interactions are increasingly recognized as playing a key role in population dynamics and life-history evolution (Dieckmann *et al.*, 2000). Experiencing the same local biotic and abiotic micro-environment will often result in the adoption or evolution of similar behaviour or life-history strategies. Furthermore, the local interactions among individuals often result in a reduction of aggression

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through familiarity and the promotion of helping behaviours. The spatial unit in which social interactions will influence heterogeneity probably is not the same as the one in which the abiotic environment will influence heterogeneity, which is itself different from the one in which the genetic divergence will be relevant. In the same way, individuals that share a common history through genetic similarities, common maternal environments, etc, often show common life history traits (Mousseau & Fox, 1998). One very natural way of assessing this type of heterogeneity is to distinguish between individuals sharing a common genetic architecture, a common family, or a common environment during development and individuals that differ by one or several of these characteristics. For example, in studies on dispersal (Clobert *et al.*, 2001), one may predict the evolution of individual heterogeneity in transition probabilities between patches when the reason for dispersal is known. If dispersal is promoted by kin competition (or inbreeding), then the within-family variance is expected to be important while the between-family variance is expected to be reduced. If the local environment influences dispersal, then the within-family variance will be reduced and the between-family variance will be more pronounced (Massot & Clobert, 2000). So, by relying on theoretical considerations and the species' biology, it might often be possible to predict, at least qualitatively, the role of space and history in shaping heterogeneity. This leads to the important question of how to deal with such predictions?

One potential way to address this question is to use information on proximity in terms of space and history to build specifically oriented goodness of fit tests. For example, one might develop an individual base version of RELEASE (Burnham *et al.*, 1987) where the capture-recapture history can be manipulated at the individual level such that the role of individuals' proximity in space and history can be rigorously assessed. Another potential method is to develop nested variance and covariance CMR models with random effects (Burnham & White, this issue) so that these factors can be taken into account. The Bayesian approach seems to offer such possibilities (Brooks, this issue and Dupuis, this issue).

Yet another potential method is to model the heterogeneity. Such a model would incorporate a theoretical approach that can be translated into some testable relationship between individual or environmental descriptors and fitness components. For example, transition probabilities (as well as other fitness components) are likely to be condition-dependent and based on actual environmental cues or on internal cues describing previous experience or history (and their interaction). The optimal way(s) to combine these sources of information at any given point in time to make a particular decision of resource allocation or of movement is largely unknown. The solution requires effort both in biological theory and in its translation into appropriate multi-site or multi-state models (Lebreton & Pradel, this issue). As suggested by Cooch *et al.* (this issue), dynamic optimization (Clark & Mangel, 2000) and adaptative dynamics (Dieckmann & Metz, in press) might offer a good way of translating theory into testable CMR models as some ultra-structural model. However, to be efficient in testing theory, one needs to select appropriate approaches. Correlative approaches are not appropriate, and only carefully planned experiments (Hairston, 1989; Schwartz, this issue) can achieve this goal.

A general remark

Up to now, the development of capture-recapture methods has tried to deal with heterogeneity at the within-species level (Fig. 1). Most evolutionary ecologists

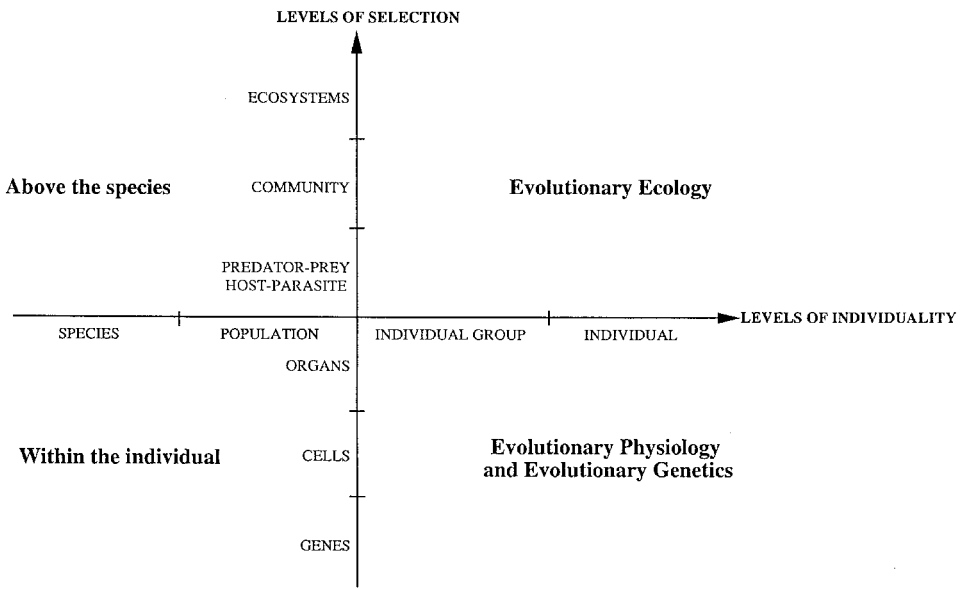


FIG. 1. Evolution of capture-mark-recapture modelling.

and evolutionists are, indeed, interested in understanding the different levels of heterogeneity and the ways they interact to shape selection and adaptation. However, heterogeneity among individuals might be influenced by higher levels of organization such as predator-prey or parasite-host interactions, between species competition, or even by ecosystems processes (Fig. 1). The feedback (coevolution) between all elements of an ecological system raises the question of the appropriate level at which selection and adaptation should be studied (Keller, 1999). Although this is still under strong debate, development of the CMR methods will prove to be interesting in this context. Indeed, applications to community dynamics, species extinction and richness, etc (Boulinier *et al.*, 1998; Nichols *et al.*, 1998), have the potential, when modified to take into account evolutionary aspects, to participate in the definition of new evolutionary concepts and tools, such as community fitness, etc, analogous to those developed at the species level (Nichols, this issue). Individuals are not only influenced by higher levels of organization but also by lower levels of organization (Dawkins, 1982). Genes, cells, etc, are all levels of organization (Fig. 1) where potential conflicts and cooperation can affect adaptation and individual selection (Michod, 1999). Up to now, there has been no opportunity to apply CMR methods to such problems. However, data are being collected on genes and gene migration which certainly have the potential to be analysed by modified versions of the actual CMR models. Mixing levels of selection is certainly a dream for any evolutionary biologist, but collecting and analysing such data must, for now, remain a challenge for the future.

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